Article

Conservation implications of forage base requirements of a marine predator population at carrying capacity

Within the graphical abstract:

What are the forage base requirements of a marine predator population at carrying capacity?

The Hawaiian Islands

Solely reef fish diet — Pelagic and reef fish diet

52% — 7%

Proportion of reef fish biomass production consumed by Palmyra Atoll's grey reef sharks, assuming a solely reef-based diet (52%) or a partially pelagic diet (7%).

Palmyra Atoll

Inform estimates

Gray reef shark populations at less remote locations are likely below their expected carrying capacity:

Expected:

Reality:

If we know the size of the forage base in a location, we can estimate how far exploited predator populations are from their expected carrying capacity, with consequences for informing ecologically viable conservation action.

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Highlights

Diet impacts the consumptive influence of gray reef sharks on reef fish resources

Some gray reef shark populations could be larger, considering their forage base

Modeling potential predator population sizes can inform their conservation
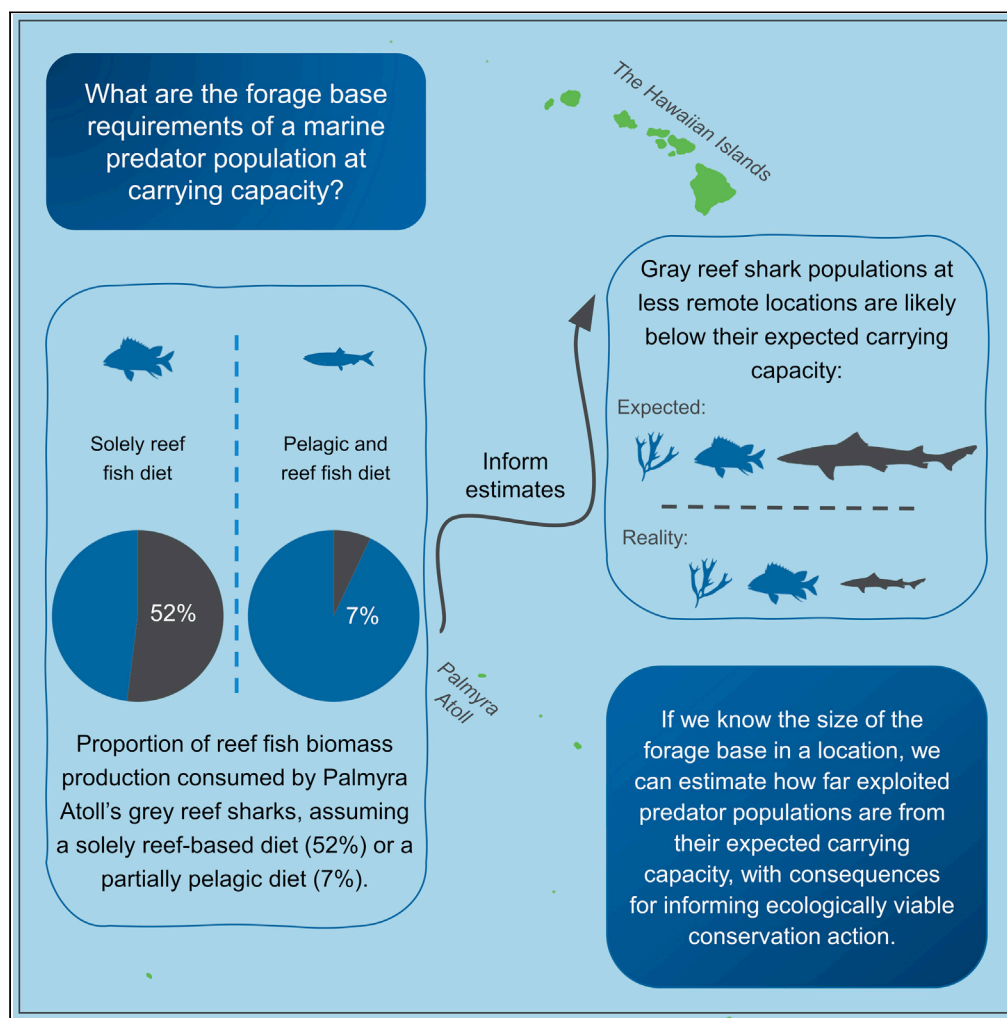
Article

Conservation implications of forage base requirements of a marine predator population at carrying capacity

Ruth E. Dunn,[1,2,4,*] Darcy Bradley,[3] Michael R. Heithaus,[1] Jennifer E. Caselle,[3] and Yannis P. Papastamatiou[1]

SUMMARY

Prey depletion may contribute to marine predator declines, yet the forage base required to sustain an unfished population of predatory fish at carrying capacity is unknown. We integrated demographic and physiological data within a Bayesian bioenergetic model to estimate annual consumption of a gray reef shark (*Carcharhinus amblyrhynchos*) population at a remote Pacific atoll (Palmyra Atoll) that are at carrying capacity. Furthermore, we estimated the proportion of the atoll's reef fish biomass production consumed by the gray reef sharks, assuming sharks either partially foraged pelagically (mean 7%), or solely within the reef environment (mean 52%). We then predicted the gray reef shark population potential of other, less remote Pacific Ocean coral reef islands, illustrating that current populations are substantially smaller than could be supported by their forage base. Our research highlights the utility of modeling how far predator population sizes are from their expected carrying capacity in informing marine conservation.

INTRODUCTION

Predatory species, situated at or near the top of ecological food webs, have the potential to play critical roles across the diversity of ecosystems that they inhabit. Conservation strategies are often focused on the protection of predators because of their importance and commonly declining population trends (Heithaus et al., 2008). Indeed, anthropogenic influences such as exploitation, land use change, habitat loss, and pollution have led to declines in many large-bodied animals and top predators worldwide (Estes et al., 2011). For example, many populations of large fishes have exhibited range contractions and biomass declines over recent decades (McCauley et al., 2015; Myers and Worm, 2003), mirroring patterns also described in terrestrial predators (Laliberte and Ripple, 2004; Ripple et al., 2016).

Throughout the marine realm, one-third of elasmobranchs are currently threatened with declining population trends (Dulvy et al., 2021). Furthermore, within a global study of more coastal systems, sharks were absent from 19% of coral reefs (MacNeil et al., 2020). These declines are often attributed to sharks having heightened vulnerability to fishing pressures because of their slow life history strategies, characterized by slow growth rates, late sexual maturity, low fecundity, and long life spans (Stevens et al., 2000). To promote the recovery of shark populations and avoid extinctions, a suite of management and conservation techniques have been encouraged (Dulvy et al., 2017). Marine protected areas (MPAs) are often advocated for as useful tools in shark conservation efforts, with MPA size, and the subsequent protection of key habitats, commonly at the forefront of considerations (Dwyer et al., 2020; Green et al., 2015).

According to ecological theory, habitat availability is not the only limiting factor to the carrying capacity of a population; resource quantity and quality are also essential to maintaining healthy population sizes (Hobbs and Hanley, 1990). Indeed, predators tend to have higher metabolic demands, necessitating an abundant, stable, and nutritious prey base (Stier et al., 2016). For example, many large terrestrial carnivores are threatened by large-scale prey depletion and a holistic approach to their conservation, that encompasses both the protection of key areas as well as prey species, has been encouraged (Wolf and Ripple, 2016). Although the importance of prey abundances to predator populations is more highly contested within marine environments, because marine species often have high dietary flexibility and spatial mobility (Free et al., 2021), there is evidence to suggest that high reef fish biomass is vital to sustaining reef shark populations (Hays et al., 2020; Tickler et al., 2017). As is the case with terrestrial carnivore conservation (Wolf and Ripple, 2016),

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the successful conservation of shark populations therefore requires an understanding of resource requirements and food web dynamics (Ferretti et al., 2018; Heupel et al., 2019), something not currently at the forefront of MPA design. Indeed, despite its conservation importance, we currently know very little regarding the forage base required to sustain healthy shark populations (MacNeil et al., 2020).

Palmyra Atoll National Wildlife Refuge is a large MPA situated within the Northern Line Islands archipelago in the central equatorial Pacific Ocean. The waters around Palmyra Atoll were first established as a National Wildlife Refuge in 2001 and its boundaries have been expanded multiple times so that it now covers an area of *ca.* 54,000 km^2. The MPA is managed by the US Fish and Wildlife Service and fishing is fully prohibited within its perimeter, with the nearest fished atolls (in the Republic of Kiribati) being several hundred kilometers away. Owing to its protected status, remote location, and subsequent lack of fishing pressure, Palmyra Atoll provides a rare and valuable opportunity to investigate the roles of marine predators in an area that has experienced minimal human impacts in comparison to most reef systems. Indeed, Palmyra Atoll's lagoons, back reefs, and fore reefs host high densities of marine predators, including blacktip reef sharks (*Carcharhinus melanopterus*), gray reef sharks (*Carcharhinus amblyrhynchos*), whitetip reef sharks (*Triaenodon obesus*), and predatory teleosts such as snappers and jacks (DeMartini et al., 2008). In particular, the gray reef shark population (estimated at *ca.* 8,300 individuals) is stable and assumed to be at, or close to, carrying capacity, having recovered from fishing pressures since the establishment of the Wildlife Refuge (details in Bradley et al., 2017b). Although the population is at carrying capacity, it is unknown what minimum forage base is required to sustain gray reef sharks at Palmyra. Furthermore, we do not know the carrying capacity of populations in other exploited locations, given similar protection.

Here, we integrate demographic and physiological data on gray reef sharks, collected over a decade of research at Palmyra Atoll, with energetics and dietary data from the literature, to construct a Bayesian bioenergetic model of the resource requirements of gray reef sharks at the atoll. We provide an estimate of the forage base needed to sustain a shark population at carrying capacity. We compared this forage base estimate to that of the annual production of reef fish biomass at Palmyra Atoll under two realistic dietary scenarios. Using these estimates of gray reef shark consumption under two scenarios, we also estimate the population potential of other, exploited locations within the native range of gray reef sharks, under current conditions.

RESULTS AND DISCUSSION

Palmyra Atoll's gray reef shark population; physiology, and demography

We quantified the forage base requirements of a population of gray reef sharks at Palmyra Atoll, which are likely at carrying capacity (Bradley et al., 2017b). The gray reef shark population is comprised of 8,344 individuals (Bayesian credible interval (CRI) = 6,977–9,698), 44% (CRI = 35–53%) of which are male and 56% (CRI = 47–65%) of which are female (Bradley et al., 2017b). Pups were not sampled, and male sharks ranged in total length from 98.5–162 cm and female sharks from 94–175 cm (Bradley et al., 2017a).

Despite the emergence of new technological tools, ecological insights into vertebrate ecology and physiology across full annual cycles remain rare. Such year-round data, however, have the potential to inform the conservation and management of large, predatory species in previously impossible ways (Dunn et al., 2020; Marra et al., 2015). Temperature, in particular, is a key parameter in determining metabolic rates and subsequent consumption estimates, both of which can vary considerably across spatial and temporal scales (Bethea et al., 2007; Dunn et al., 2020). Our biotelemetry data revealed seasonal changes in gray reef shark body temperature (GAMM result: F = 3739.4, df = 12, p < 0.05; Figure 1B). Despite this evidence of seasonality, differences in body temperature values over the course of the annual cycle were small, being lowest in March to April (mean ± SD = 28.1 ± 0.04°C), and only reaching a 'peak' of 28.9 ± 0.05°C in September to November (Figure 1B). Because of its equatorial location, seasonality in water temperatures at Palmyra Atoll is limited, and gray reef shark body temperatures, metabolic rates, and energy consumption requirements were therefore relatively constant throughout the annual cycle.

Gray reef shark energy requirements and resource consumption

We integrated body temperature and demographic data from the Palmyra Atoll gray reef shark population with energetics and dietary data for this species, or closely related species, from the literature. Using these data, we constructed a Bayesian bioenergetic model of the resource requirements of sharks at the atoll, therefore estimating the energetic resources needed to sustain a shark population at carrying capacity.
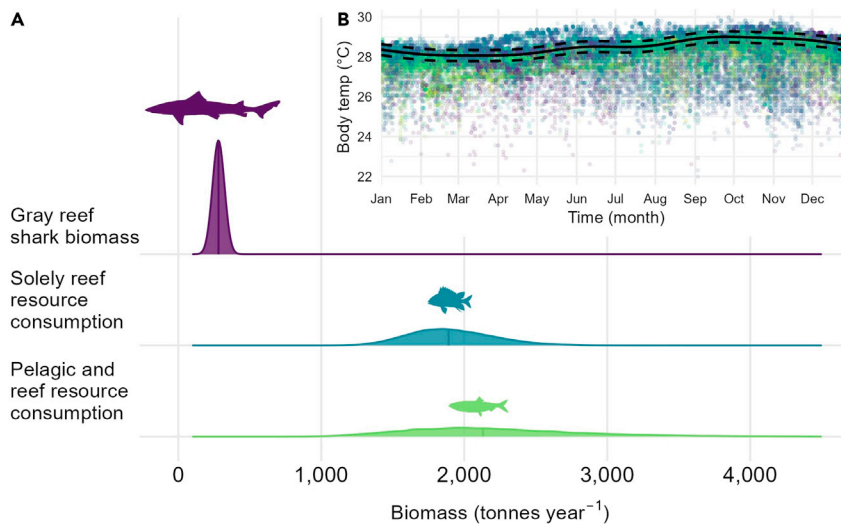
Figure 1. Estimates of the biomass of gray reef sharks at Palmyra Atoll as well as their annual prey consumption and seasonal changes in their body temperature

(A) Density plots show the posterior distributions of the estimated gray reef shark biomass (in tonnes; purple) as well as their prey consumption (in tonnes of prey consumed by the population of gray reef sharks per year), under two dietary scenarios: 1) sharks obtained energy from solely reef-associated resources (shown in blue); 2) sharks derived 86% of their diet from pelagic resources and the remaining proportion from the reef (shown in green). The vertical lines within the density plot areas illustrate the mean estimated values.

(B) Mean estimated smoothing function of Julian day (solid line) and shark body temperature (determined from acoustic telemetry) with upper and lower confidence intervals at two standard errors above and below the mean (dashed lines) from a generalized additive mixed model. The raw data are presented as points, colored by individual shark.

Figure prepared with R packages ggplot2 (Wickham, 2016), *ggridges* (Wilke, 2021), *rphylopic* (Chamberlain, 2020), *and viridis* (Garnier et al., 2021).

Monte Carlo simulations were used to account for uncertainty associated with the input values required by the bioenergetic model (Barnett et al., 2017). We estimated the annual energy consumption of the gray reef shark population at Palmyra Atoll to be 12.48 GJ (CRI = 9.19–16.01), with individuals consuming a mean of 2.12% of their body mass each day (CRI = 1.26–3.15%). These daily rations are similar to predictions for a sub-population of gray reef sharks in French Polynesia (1.19–1.92% body mass day^{-1}), calculated using a similar bioenergetics model (Mourier et al., 2016).

We converted our estimates of annual gray reef shark energy consumption into estimates of biomass consumption. Initially, we assumed that gray reef sharks obtained their energy solely from reef-associated resources and that they consumed a highly piscivorous diet (Papastamatiou et al., 2006; as in Wetherbee et al., 1997). Our estimates showed that when gray reef sharks consumed a solely reef-based diet, their consumption equated to a forage base of 1,914 tonnes year^{-1} (CRI = 1,355–2,514; Figure 1A). We then compared this gray reef shark forage base estimate to that of the annual production of reef fish biomass at Palmyra Atoll, a dynamic measure of the potential for biomass growth (Bellwood et al., 2019). According to metabolic theory, annual reef fish biomass production within the reef habitat surrounding Palmyra Atoll (3,967 ha^2) was 10 tonnes day^{-1}, equivalent to 3,651 tonnes year^{-1} (Figure 2). Annual reef fish biomass production at Palmyra Atoll therefore equated to 0.92 tonnes ha^{-1} (Figure 3B), similar to the average biomass of *ca.* 1 tonnes ha^{-1} that unfished reefs are able to support (MacNeil et al., 2015). If they were to have consumed a diet composed solely of reef-based resources, the Palmyra gray reef shark population would therefore have consumed a mean of 52% of annual reef fish biomass production (CRI = 37–69%; Figure 2). Although gray reef sharks are the most abundant predator at Palmyra in terms of biomass (McCauley et al., 2012a), other large predatory species, such as blacktip reef sharks and two-spot red snappers (*Lutjanus bohar*), are also likely to have extracted a proportion of Palmyra Atoll's reef fish resources (McCauley et al., 2012b). Currently, the population sizes of the other large predatory fishes at Palmyra are unknown, and so we are unable to infer the scale of their consumptive influence. Indeed, although trophic interaction models have suggested that shark consumption may not be an important driver of top-down ecosystem dynamics within coastal habitats (e.g., Stevens et al., 2000), these models frequently lack accurate
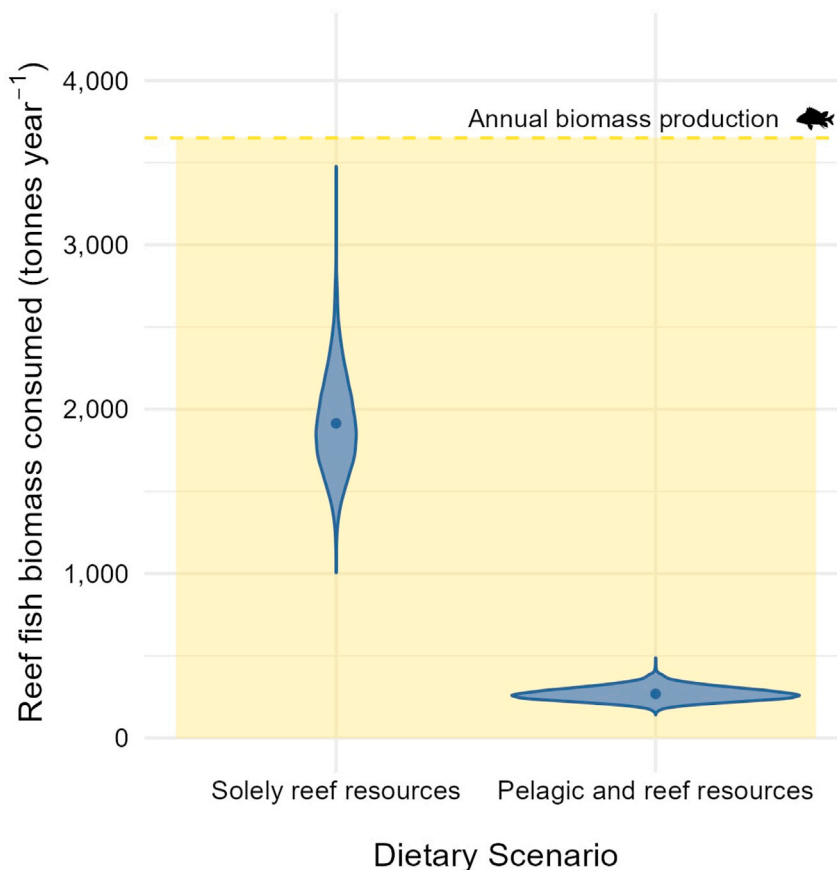
Figure 2. Proportion of the annual reef fish biomass production at Palmyra Atoll that is consumed by gray reef sharks

Violin plots show the posterior distributions of the reef fish biomass consumed by the population of gray reef sharks per year when they (A) obtained 100% of their energy from reef-associated resources and (B) obtained 14% of their diet from reef-associated resources and the remaining proportion from pelagic resources. The blue points illustrate the mean estimated values. The dashed, yellow, horizontal line identifies the annual reef fish biomass production at Palmyra Atoll. *Figure prepared with R packages ggplot2 (Wickham, 2016) and rphylopic (Chamberlain, 2020).*

population size estimates. Contrastingly, bioenergetic models that account for high shark abundance may be able to further elucidate the potential importance of sharks as drivers of top-down ecosystem dynamics within coastal habitats (Barnett et al., 2017).

Although gray reef sharks appear to be reliant on coastal reef environments in many locations (Barnett et al., 2012; Heupel et al., 2010; Vianna et al., 2013), at Palmyra Atoll they obtain 86% (CRI = 0.81–0.91%) of their energy from pelagic resources (McCauley et al., 2012b), thereby transporting energy and nutrients between offshore waters and near-shore reefs (Williams et al., 2018). When Palmyra's gray reef sharks were assumed to have extracted a large proportion of their resources from the pelagic environment, they consumed a total biomass of 2,266 tonnes year^{-1} (CRI = 1,109–3,478; Figure 1A). Of this, gray reef sharks extracted 268 tonnes year^{-1} (CRI = 190–350) from reef resources (7% (CRI = 6–9%) of annual reef fish biomass production at Palmyra Atoll; Figure 2) and 1,998 tonnes year^{-1} (CRI = 893–3,344) from pelagic resources. The role of wide-ranging predators in energy and nutrient transfer across ecosystem boundaries – via excretion or egestion after prey consumption (Schmitz et al., 2010) – may vary both spatially, across the predator's range, as well as temporally, because of seasonality in predator movements and prey abundances (Dowd et al., 2006; Forcada et al., 2009). Although gray reef sharks at Palmyra may transfer significant amounts of nutrients to reefs from pelagic ecosystems, sharks in other studied locations may not make as much use of pelagic food sources, and instead rely on predominantly inshore coastal food webs (Heupel et al., 2018; Speed et al., 2012).
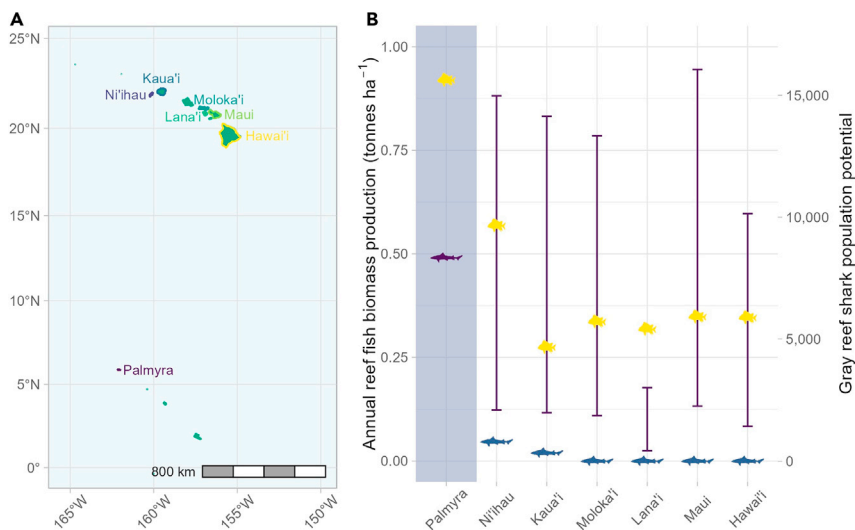
Figure 3. Annual reef fish production at Palmyra Atoll and the main Hawaiian Islands as well as the size of gray reef shark population that the Hawaiian Islands have the potential to support, and the populations sizes that they currently support

(A) Locations of Palmyra Atoll and six of the main Hawaiian Islands.

(B) Annual reef fish production (yellow fish symbols) at Palmyra Atoll (highlighted in blue) and six of the main Hawaiian Islands. The gray reef shark population size at Palmyra is shown (purple shark symbol). The potential gray reef shark population sizes that the main Hawaiian Islands could support are illustrated with purple error bars spanning from i) if the population was assumed to consume 52% of reef fish biomass, assuming that these populations obtained their diet solely from reef-associated resources (Wetherbee et al., 1997) (lower limit), to ii) if the population was assumed to consume 7% of reef fish biomass, assuming that these populations obtained their diet from both pelagic-associated and reef-associated resources (McCauley et al., 2012b) (upper limit). Shark density estimates from towed-diver surveys (Nadon et al., 2012) were multiplied by reef habitat availability to illustrate current gray reef shark population estimates at the main Hawaiian Islands (blue shark symbols).

Figure prepared with R packages ggplot2 (Wickham, 2016), rphylopic (Chamberlain, 2020), and viridis (Garnier et al., 2021).

Obtaining trophic subsidies from adjacent ecosystems is a key mechanism through which top-heavy biomass pyramids, composed of high upper trophic level predator biomasses in comparison to those of lower trophic level species, can exist (Trebilco et al., 2013). For example, over a short time frame, a large biomass of gray reef sharks within a lagoon in French Polynesia is supported by transient spawning aggregations of reef fish in addition to prey obtained from surrounding reef areas (Mourier et al., 2016). At Palmyra Atoll, there has been debate regarding whether the near-pristine environment is host to a top-heavy trophic pyramid structure; initial estimates suggested an inverted biomass pyramid (Sandin et al., 2008), but subsequent estimates suggest lower predator biomasses (Bradley et al., 2017b). We found that, when consuming a diet that was composed of 86% pelagic resources, the gray reef shark population would have only consumed a mean of 7% (CRI = 6–9%) of the reef fish biomass production around the atoll (Figure 2A). If pelagic prey are not included in calculations of the biomass of resource species, top-heavy biomass pyramids along the forereef may therefore be plausible; however, such a pyramid would disappear should the full prey base supporting gray reef shark diets be included in calculations. Indeed, high predator biomasses on coral reefs, supported by external subsidies, including those from pelagic or lagoon ecosystems, may be a more common feature of healthy reef ecosystems than previously thought (Skinner et al., 2021).

Gray reef shark population potential at the main Hawaiian Islands

Although the marine environment surrounding Palmyra Atoll is protected and therefore exposed to negligible fishing pressure (White et al., 2017), many coral reef systems throughout the world do not have this protection. For example, the main Hawaiian Islands (*ca.* 1,700 km from Palmyra Atoll) are urbanized, heavily populated, and subject to a range of anthropogenic influences including pollution, habitat degradation and intensive fishing pressure (Papastamatiou et al., 2006). The main Hawaiian Islands are within the gray reef sharks' native range, but populations are assumed to be small; densities of <0.069 sharks ha^{-1}

Table 1. Estimates of the size of gray reef shark population that the 6 of the main Hawaiian Islands have the potential to support, as well as estimates of their current populations sizes

Island	Upper population estimate	Lower population estimate	Current population estimate (from Nadon et al., 2012)
Niʻihau	14,982	2,097	795
Kauaʻi	14,144	1,980	337
Molokaʻi	13,341	1,867	0
Lānaʻi	3,009	421	0
Maui	16,069	2,249	0
Hawaiʻi	10,151	1,420	0

The potential gray reef shark population sizes that main Hawaiian Islands could support assuming firstly that the populations consumed 7% of reef fish biomass, assuming that these populations obtained their diet from both pelagic-associated and reef-associated resources (McCauley et al., 2012b) and secondly that the populations consumed 52% of available reef fish biomass, assuming that these populations obtained their diet solely from reef-associated resources (Wetherbee et al., 1997). Shark density estimates from towed-diver surveys (Nadon et al., 2012) were multiplied by reef habitat availability to illustrate current gray reef shark population estimates at the main Hawaiian Islands.

were observed during towed-diver surveys (Nadon et al., 2012), and true densities and biomasses may be substantially lower (Bradley et al., 2017b). By combining our knowledge of the reef fish biomass consumption of gray reef sharks under two dietary scenarios, with data on the biomass of reef fish across 6 of the main Hawaiian Islands, we were able to estimate the gray reef shark population potential of these islands under current conditions (Table 1). Reef fish biomass production across the main Hawaiian Islands was significantly lower than at Palmyra Atoll (Figure 3B) and was highest at Niʻihau (0.57 tonnes ha^{-1}), the most northerly and least populated of the main Hawaiian Islands (population *ca.* 100 people). Low reef fish biomasses throughout Hawaiʻi are likely due to heightened anthropogenic pressures, including drivers like habitat degradation and fishing activity (Friedlander and DeMartini, 2002). Nevertheless, the Hawaiian Islands do host large areas of reef habitat (ranging from 4,122–22,463 ha at Lānaʻi and Kauaʻi, respectively) meaning that, theoretically, the Hawaiian Islands could have the capacity to support substantially larger populations of gray reef sharks than are currently present (Figure 3B). Indeed, across all the main Hawaiian Islands, our estimates of gray reef shark population potential are much larger than the numbers of sharks seen during dive surveys, with our estimates ranging from a minimum of 421–3,009 individuals in Lānaʻi, to 2,249–16,069 in Maui (Table 1; Figure 3B). The observed small gray reef shark population sizes, lower than those predicted from the available forage base, suggest that anthropogenic or biotic factors (e.g., competition) are currently limiting population sizes below their carrying capacities. For example, at the main Hawaiian Islands, there are large populations of sandbar sharks (*Carcharhinus plumbeus*) which have high dietary overlap with gray reef sharks, likely causing interspecific competition and spatial segregation in the species' distributions (Papastamatiou et al., 2006).

Conclusion

Although a suite of management and conservation techniques are used to aid the recovery and restoration of marine predator populations (Dulvy et al., 2014, 2017), they rarely consider resource quantity and quality, despite these metrics being critical to knowing what population sizes are even possible to be restored. Indeed, obtaining population-level prey consumption estimates for large predators is challenging because requisite parameters for bioenergetic models are often not available (Barnett et al., 2017). This is particularly true of predators that inhabit the marine environment, because of their large ranges and cryptic natures (Williams et al., 2004). Our results are therefore useful in informing the quantity of reef fish biomass production needed to support a shark population at carrying capacity. We demonstrate that at Palmyra Atoll, because of their reliance on pelagic subsidies, the gray reef shark population consumes little of the available reef fish biomass. In other locations, where pelagic subsidies are not used, gray reef sharks are likely to consume a much larger proportion of reef fish production. Our model also suggests that current gray reef populations at other Pacific islands are likely far below the carrying capacity when considering forage base availability.

More than one-third of sharks, rays, and chimeras are currently threatened with overfishing because of their slow life history strategies, including slow growth rates, late sexual maturity, low fecundity, and long life

spans (Dulvy et al., 2021; Stevens et al., 2000). Furthermore, a global study demonstrated an absence of sharks from 19% of coral reefs (MacNeil et al., 2020), with sharks that inhabit tropical, coastal waters being particularly ar risk of extinction because of high intensity fishing pressure and a lack of depth refuge (Dulvy et al., 2021). Our results demonstrate that, given appropriate protection from fishing pressures, biomasses of predators, such as the endangered and declining gray reef shark (Simpfendorfer et al., 2020), could be much larger than they currently are. Indeed, despite a lack of a species-specific management plan, current conservation advice regarding the recovery of gray reef shark populations is focused on the implementation of marine protected areas, particularly around coral reef habitats (Simpfendorfer et al., 2020). Parameterizing bioenergetic models with the sizes of recovered predator populations that inhabit such protected areas, allows the estimation of how far exploited populations are from their expected carrying capacity, with consequences for informing ecologically viable conservation action.

Limitations of the study

The focus of our study is a single population of gray reef sharks, because of a lack of accurate population estimates for the other predatory species within the system at Palmyra Atoll and elsewhere. Obtaining population size estimates of the other predatory sharks and teleosts at Palmyra Atoll would provide a more complete overview of the role of predators and their combined consumptive effects within unfished coral reef habitats. Furthermore, insights into the species-specific and location-specific diets of predator populations, as well as the community composition of the available prey, would increase the transferability of this approach between locations.

Although we calculated the prey requirements of the population of gray reef sharks at Palmyra to the best of our ability, it is likely that there are different energetic costs associated with foraging within the reef environment, as opposed to foraging offshore. Future studies could therefore seek to use telemetry data to investigate the energetic trade-off between these contrasting foraging strategies, particularly for gray reef sharks that exhibit a known tendency to return to a central place (Papastamatiou et al., 2018b).

STAR★METHODS

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  - Shark population potential at the main Hawaiian Islands

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2021.103646.

AUTHOR CONTRIBUTIONS

Conceptualization, R.E.D, Y.P.P., and M.R.H; Data curation, Y.P.P., D.B., and J.E.C.; Formal Analysis, R.E.D.; Funding acquisition, Y.P.P., and M.R.H.; Investigation, Y.P.P., D.B., and J.E.C.; Supervision, Y.P.P and M.R.H.; Visualization, R.E.D.; Writing – original draft, R.E.D.; Writing – review & editing, Y.P.P., M.R.H, D.B., and J.E.C.

DECLARATION OF INTEREST

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Gray reef shark length data	Bradley et al., 2017a, 2017b	https://doi.org/10.1371/journal.pone.0172370
Gray reef shark body temperature data	Papastamatiou et al., 2018a, 2018b	https://doi.org/10.1186/s40462-018-0127-3
Length-mass scaling constants	FishBase	https://www.fishbase.se/
Gray reef shark prey items – energy densities	This study	Table S2
Reef fish biomass data	McCoy et al., 2016	http://doi.org/10.7289/V5G73BQJ
Software and algorithms		
R software	R Core Team, 2020	https://www.r-project.org/
JAGS software	Plummer, 2003	https://mcmc-jags.sourceforge.io/
R package mgcv	Wood, 2017	https://cran.r-project.org/web/packages/mgcv/index.html
R package runjags	Denwood, 2016	https://cran.r-project.org/web/packages/runjags/index.html
Original JAGS code	This study	Data S1

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources should be directed to Ruth Dunn (ruthelizabethdunn@gmail.com).

Materials availability
- Gray reef shark length data were generated by (Bradley et al., 2017a).
- Gray reef shark body temperature data were generated by (Papastamatiou et al., 2018b).
- Reef fish biomass data were generated by (McCoy et al., 2016).

Data and code availability
The energy densities of gray reef shark prey items are listed in this paper's Table S2. The original JAGS code is available in this paper's Data S1. Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Gray reef sharks
In this study we researched gray reef sharks (*Carcharhinus amblyrhynchos*). We used data from 1,370 individual adult sharks of which 899 were female and 471 were female.

METHOD DETAILS

Ethical statement
This project was certified and all sampling protocols were approved by the Institutional Animal Care and Use Committee (IACUC), University of California Santa Barbara (permit number 856, date of IACUC

approval: 5/31/2012) and was permitted by the US Fish and Wildlife Service (USFWS) special permits (permit numbers #12533–14,011, #12533–13,011, #12533–12,011, #12533–11,007, #12533–10,011, #12533–09010, #12533–08011, and #12533–07006).

Data collection

Fieldwork took place at Palmyra Atoll, in the central Pacific Ocean (5°54′N, 162°05′ W). Between October 2006 and October 2014, gray reef sharks (n = 1,370) were caught on hook and line, sexed, measured and dart tagged below the dorsal fin (details in Bradley et al., 2017a). Pups were not sampled, and we therefore obtained data from the adult and sub-adult proportion of the population only. Capture and tagging data were used to quantify size frequency and sex ratios, growth rates, and population size (Bradley et al., 2017a, 2017b).

Ectothermic predator metabolic rates (and therefore consumption rates) will be temperature dependent and will change seasonally. To obtain long term body temperature data of gray reef sharks at Palmyra, we caught sharks (n = 12) and restrained them adjacent to the boat. Sharks were inverted to induce tonic immobility, a trance like state, and a small incision was made in the ventral surface. We then implanted a Vemco V16PT transmitter and closed the suture with uninterrupted sutures. Tags transmit an acoustic signal (69 KHz) which can be detected by a network of underwater listening stations (VR2W) placed throughout the atoll. Every time a shark is within range of a listening station (300-500 m dependent on location), the VR2W records the unique transmitter number, time/date of detection, body temperature, and swimming depth. VR2Ws were downloaded annually, and redeployed after switching out batteries (for more details see Papastamatiou et al., 2018a; 2018b).

QUANTIFICATION AND STATISTICAL ANALYSIS

Bioenergetic modelling

We developed a Bayesian bioenergetic model to estimate the total energy required by the population of gray reef sharks at Palmyra Atoll. Initially we sought to estimate $C_{i,j}$ the energy required by an individual i at day j, where j ranged from 1 – 366 and corresponded with a time series from the 1st January to the 31st December.

To describe the energy required by an individual gray reef shark on a given day $C_{i,j}$ (kJ), we used a gamma model, suitable for a continuous, non-negative variable. The equation to describe the mean daily energy requirements of each individual $\bar{U}_{i,j}$ was based on an energy balance equation previously used for other shark species (Manishin et al., 2019; Schindler et al., 2002; Wood et al., 2009):

$$\bar{U}_{i,j} = A_{i,j} + D_{i,j} + E_{i,j} + G_{i,j} + R_{i,j} \qquad \text{(Equation 1)}$$

Here, $A_{i,j}$ was daily routine metabolism (as gray reef sharks are obligate ram ventilators and are required to swim in order to obtain sufficient oxygen), $D_{i,j}$ was daily energy used for digestion (specific dynamic action), $E_{i,j}$ was energy that was lost daily to waste (excretion and egestion), $G_{i,j}$ was energy allocated daily towards growth and $R_{i,j}$ was energy allocated towards reproduction.

We used a gamma link function to incorporate unexplained stochasticity around the mean daily energy required for each individual (Equation 1) as follows:

$$C_{i,j} \sim gamma\left(r_{i,j},\ \lambda_{i,j}\right) \qquad \text{(Equation 2)}$$

The expectation of the shape r and rate λ parameters describing this gamma distribution reflected the mean daily energy required $\bar{U}$. The precision φ of these parameters, represented residual environmental stochasticity around the mean and was assigned from a normal prior distribution with a mean of 100 kJ day^{-1} and a standard deviation of 10 kJ day^{-1} (Table S1).

First, the mass M_i of the 1,370 sharks that we obtained length measurements from were calculated using measurements of total length L_i and length-mass scaling constants a (0.00878) and b (3.050) from FishBase (Froese and Pauly, 2020) as follows:

$$M_i = aL_i^{\ b} \qquad \text{(Equation 3)}$$

We assumed the mass of each individual remained constant throughout the year. Routine metabolic rate $A_{i,j}$ was then calculated using an equation for ectothermic sharks (Payne et al., 2015):

$$log_{10}A_{i,j} = 0.79 log_{10}M_i + 2.31 \qquad \text{(Equation 4)}$$

Values of hourly metabolic rate (mg O_2 h^{-1}) were transformed into daily metabolic rate (kJ day^{-1}) using an oxycalorific coefficient of 14.6 J mg O_2^{-1} (Brett and Groves, 1979; Lowe, 2002). To correct daily metabolic rates for seasonal changes in gray reef shark body temperature, we implemented a generalised additive mixed model (GAMMs) using the *mgcv* package (Wood, 2017) in R version 4.0.3 (R Core Team, 2020). We fitted the GAMM using a Gaussian distribution with an identity link function to model shark body temperature. Julian day was included as a smoothing function because of its many levels (n_{days} = 366). Individual shark, receiver ID, and hour of the day were modelled as random effects with random intercepts to account for the data's dependency structure (Zuur et al., 2014). We validated the fit of the model by plotting the residuals against the fitted values and the model covariates, checking for violation of homogeneity (Zuur et al., 2014). We used the mean smoothing function of Julian day from this GAMM to correct for non-linear seasonal changes in body temperature and a prior for Q_{10} (mean 2.325 with a standard deviation of 0.3; Table S1) that encompassed the range of values (1.65 – 3.2) seen within tropical sharks (Bernal et al., 2012).

Due to a lack of empirical data on digestion (specific dynamic action) $D_{i,j}$ and excretion (including both faeces and urine) $E_{i,j}$, we specified informative priors, *d* and *e* respectively (Table S1). The prior for *d* (mean 12.52% of $C_{i,j}$ with a standard deviation of 3.9%) was informed by the cost of specific dynamic action in adult lesser spotted dogfish *Scyliorhinus canicular* (Sims and Davies, 1994). The prior for *e* (mean 27% of $C_{i,j}$ with a standard deviation of 5.42%) was informed by the generally accepted value for carnivorous fishes and elasmobranchs (Brett and Groves, 1979).

The daily energy required for somatic growth $G_{i,j}$ was calculated as follows:

$$G_{i,j} = Ta(L_i + k(L_\infty - L_i))^b - aL_i^b \Big/ 366 \qquad \text{(Equation 5)}$$

Here, *T* was the energy density of shark tissue, the prior for which (mean 6.07 kJ g^{-1} with a standard deviation of 1.55 kJ g^{-1}; Table S1) was informed by the calorific value of scalloped hammerhead sharks *Sphyrna lewini* pups (Lowe, 2002). Additionally, *k* was the von Bertalanffy growth coefficient (0.05) and L_∞ was the asymptotic length (163.3 cm) of the Palmyra gray reef shark population (Bradley et al., 2017a).

We assumed that male and immature female sharks invested negligible energy in reproduction. In mature females, $R_{i,j}$ was estimated from the annual growth of reproductive tissue/embryos by combining pup mass at birth. The energy that females allocated towards reproduction each day was therefore calculated from a pub length L_p value of 67 cm (White, 2007) and a prior for average litter size *l* (mean 4 with a standard deviation of 0.5; Table S1) that ranged between 3-6 (Wetherbee et al., 1997), as follows:

$$R_{i,j} = TaL_p^b l \Big/ 366 \qquad \text{(Equation 6)}$$

We extrapolated from the daily individual energy requirements to the annual energy requirements of the whole population by summing the $C_{i,j}$ values from the 1,370 measured individuals by a prior for the sex ratio *s* (mean of 0.44 male with a standard deviation of 0.05; Table S1) and the total population size *P* (mean of 8,344 with a standard deviation of 500; Table S1) of the Palmyra gray reef shark population (Bradley et al., 2017b). We also accounted for the proportion of females that were immature *i*, with a prior distribution (mean of 0.109 with a standard deviation of 0.05; Table S1) based on the fact that 10.9% of the females caught and measured were smaller than 126 cm, the predicted size of maturity (Bradley et al., 2017a).

We converted annual gray reef shark energy consumption estimates into estimates of biomass by combining the energy density values of prey items within two hypothetical diet proportion scenarios: 1) gray reef sharks obtained energy solely from reef-associated resources (Wetherbee et al., 1997), and 2) gray reef sharks derived 86% of their biomass from pelagic resources and the remaining 14% from the reef (McCauley et al., 2012b). Gray reef sharks that obtain their prey from the reef are highly (>80%) piscivorous, with cephalopods and crustaceans accounting for the remainder of their diets (Papastamatiou et al., 2006; Wetherbee et al., 1997). Contrastingly, gray reef sharks that feed in pelagic habitats have been observed to feed on aggregations of Clupeid fishes (McCauley et al., 2012b). The prior distributions for

the energetic density of reef-associated resources and pelagic-associated resources (Table S1) were therefore composed of energy density values of a range of prey items (Table S2). A reef-associated diet was assumed to be composed of 85% fish f (mean 6.6 kJ g^{-1} with a standard deviation of 1 kJ g^{-1}) and 15% molluscs and crustaceans o (mean 4.2 kJ g^{-1} with a standard deviation of 0.4 kJ g^{-1}), whilst a pelagic-associated diet was composed of pelagic fish p (mean 5.84 kJ g^{-1} with a standard deviation of 1.66 kJ g^{-1}).

The bioenergetic model was fitted using JAGS (Plummer, 2003) using the *runjags* interface in R (Denwood, 2016) with a burn-in of 400 plus 1,000 adaptive iterations for 10,000 iterations to achieve convergence. Convergence was evaluated via visual inspection of the chains. The JAGS code is presented in Data S1.

Reef fish biomass at Palmyra Atoll and the main Hawaiian Islands

Reef fish biomass at Palmyra Atoll and 6 of the main Hawaiian Islands (Hawai'i, Maui, Lāna'i, Moloka'i, Kaua'i and Ni'hau) were estimated using data collected via underwater visual stationary point counts as part of the Pacific Reef Assessment and Monitoring Program between 2010 and 2019 (McCoy et al., 2016). The abundance and size of all reef fish species were estimated and recorded across 15 m diameter survey sites within reef habitat across the extent of Palmyra Atoll and the Hawaiian Islands. We restricted our analysis to exclude shark and ray data and only analyse fish that were >12.5 cm and which were therefore representative of shark prey size ranges (Mourier et al., 2016). Reef fish biomass per unit area B was then calculated using length-weight conversion factors from FishBase (Froese and Pauly, 2020). We converted reef fish biomass into the rate of annual fish production per unit area F using metabolic theory (Brown et al., 2004; Ernest et al., 2003; Jennings et al., 2008), where the rate of new biomass production through growth and reproduction are dependent on body mass and temperature as follows:

$$F = \exp\left(25.22 - \frac{E}{kt}\right)B^S \qquad \text{(Equation 7)}$$

Here, E is the activation energy of metabolism (0.63 eV), k is the Boltzmann's constant (8.62 × 10^{-5} eV Kelvin^{-1}), t is the absolute temperature in Kelvin (28.5°C + 273) and S is the scaling exponent for the relationship between fish body mass and biomass production (0.761). We then extrapolated this rate of annual fish production to the area of reef habitat available at Palmyra Atoll and the main Hawaiian Islands (Figure 3).

Shark population potential at the main Hawaiian Islands

We estimated the potential population sizes of gray reef sharks at the main Hawaiian Islands based on the proportion of reef fish biomass in the diet of gray reef sharks at Palmyra Atoll under the two dietary scenarios. First, using these two proportions, we calculated the reef fish biomass that similarly stable populations of gray reef sharks might be able to consume at the main Hawaiian Islands. We then divided this value by the annual energy requirements of a single gray reef shark to estimate the potential population sizes that the main Hawaiian Islands could support, given the reef habitat and reef fish biomass production available. We compared these estimates with those of current gray reef shark population sizes by multiplying shark density estimates from towed-diver surveys (Nadon et al., 2012) with reef habitat availability.